TRICHOME MORPHOLOGY IN SELECTED MEXICAN RED OAK SPECIES (*QUERCUS* SECTION *LOBATAE*)

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ABSTRACT

Mature leaves and twigs from thirty red oak species, mostly endemic to Mexico, were examined with SEM to assess trichome morphology. Ten trichome types were identified: two glandular and eight nonglandular. Described for the first time in the oak literature are fasciculate contorted, fasciculate crested, and multiple stellate trichomes. Furthermore, three trichome types are reported for the first time in red oaks: stellate, fused stellate, and glandular branched. The most common types on the twigs examined are fasciculate sessile and multiradiate trichome while the most frequent types on the abaxial leaf surfaces are fasciculate sessile, fasciculate stipitate, and multiradiate trichomes. In contrast to the significant morphological variation found in oak leaf shape, trichome complements within each species are nearly invariable and therefore useful in the identification of most species. In summary, together with vegetative and reproductive characters, trichome morphology provides additional information for the identification and characterization of Mexican oak species.

RESUMEN

Hojas maduras y ramillas de treinta especies de encinos rojos, principalmente endémicos a Mexico, fueron examinadas con microscopía electrónica de barrido para evaluar la variación morfológica de tricomas. En este trabajo se identificaron diez tipos de tricomas: dos glandulares y ocho no glandulares. De estos, se describen por primera vez para encinos los tricomas fasciculado contorto, fasciculado crestado y estrellado multiple. Además, se reportan por primera vez para encinos rojos tres tipos de trichomes: estrellado, estrellado fusionado y glandular ramificado. Los tipos de trichoma más comunes en ramillas son el fasciculado sésil y el multiradiado, mientras que en el envés de las hojas los tipos de tricoma más frecuentes son el fasciculado sésil, fasciculado estipitado y el multiradiado. Aunque los encinos muestran una gran variación en morfología foliar, los tipos de tricomas presentes en cada especie son constantes y por lo tanto son muy útiles en la identificación de la mayoría de las especies. En resumen, los caracteres vegetativos y reproductivos junto con la morfología de trichomes proporcionan información valiosa para la identificación y caracterización de las especies Mexicanas de encino.

INTRODUCTION

The genus *Quercus* (Fagaceae) consists of approximately 400 species of trees and shrubs distributed in temperate and subtropical regions of the Northern Hemisphere. In the Americas, *Quercus* is found from southern Canada to Colombia with representatives of three sections within the subgenus *Quercus*: *Quercus* (white oaks), *Protobalanus* (intermediate oaks), and *Lobatae* (red oaks) (Nixon 1993). Due to the large diversity of white and red oaks, Mexico is considered the center of diversity for the genus in the New World (Rzedowski 1965; Nixon 1993).

The number of red oak species has been estimated around 195 (Jensen 1997) with about 55 species endemic to Mexico (Nixon 1993). In his treatment on the American oaks, Trelease (1924) segregated the red oak species into 73 series and also proposed a classification based on leaf and fruit morphology. However, his hypothesis on the relationships of red oak species has not been tested with phylogenetic methods. Although the mono-

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phyly of the red oak section is well supported (Nixon 1984; Manos 1999), an intrasectional phylogeny for the red oaks is yet to be conducted. As in other oak groups, Mexican oak species are difficult to study because most of them show significant amounts of foliar polymorphism. Species identity becomes even more complex when either hybridization or introgression has taken place. Therefore, taxonomic problems in many oak species persist, particularly in those species that have similar or overlapping leaf morphology.

The utility of trichome morphology for species identification has been demonstrated in several plant families such as Brassicaceae, Geraniaceae, and Sterculiaceae (Inamdar & Rao 1983; Metcalfe & Chalk 1950; Oosthuizen 1983; Shanmuka Rao 1987). In oaks, trichome characterization has been carried out for several eastern North American, Asian, and European species. The first study on trichome morphology of eastern North American oak species was reported by Dyal in 1936, who classified them, based on secretory function, into glandular and nonglandular. Camus (1934–1953) described seven trichome types that fall into the glandular and nonglandular categories previously described by Dyal (1936). Hardin (1976) published the first comprehensive work on oak trichome morphology for 58 eastern United States (US) oak species and recognized 10 trichome types. Thomson and Mohlenbrock (1979), Jones (1986), and Manos (1993b) conducted similar studies on other U.S. oak species. Trichome morphology of European and Mediterranean oak species has also been extensively documented by several authors (Olsson 1976; Kissling 1977, 1993; Safou & Saint-Martin 1989; Gellini et al. 1992; Llamas et al. 1995; Bussotti & Grossoni 1997). Trichome morphology, together with other vegetative and reproductive characters, has been used to discriminate several U.S. oak species, as well as a few Mexican species distributed in the northwest of the country (Tucker 1952; Tucker & Muller 1957; Nixon & Steele 1981; Spellenberg 1992, 1998; Nixon & Muller 1993; Bacon & Spellenberg 1996). However, to date, no in-depth research on the trichome morphology of Mexican taxa has been carried out. Several regional taxonomic treatments of Mexican oak species have been conducted (González 1986; Valencia 1989; Vázquez 1992, 2000; Spellenberg et al. 1998; Spellenberg 2001), but none of them has characterized trichome diversity. Only a few authors have discussed the potential utility of trichome types for identification of Mexican species (McVaugh 1974; Rzedowski & Rzedowski 1979; Vázquez 1992). Accordingly, the objective of this study is to characterize the trichome morphology from twigs and leaves from thirty Mexican red oaks, mainly endemic to Mexico, using scanning electron microscopy (SEM). Detailed examination of these species revealed the presence of ten trichome types: four of these trichomes have been previously described, three of them represent entirely new trichome types, and the remaining three are trichome types not previously documented for red oaks. Each species examined shows a particular trichome complement which, together with other vegetative and reproductive characters, provides useful information for species identification and characterization.

MATERIALS AND METHODS

Leaves and twigs from thirty species of red oak species chiefly endemic to Mexico were selected for examination of trichome morphology under SEM. Nixon (1993) has reported 41 red oak species endemic to Mexico, of which, twenty-one have persistent indument and were sampled in this study. Two additional species with persistent indument (*Q. castanea* and *Q. crassifolia*) whose range extends to Central America were included in this study because they are widely distributed in Mexico. For comparison, six glabrous

TABLE 1. Red oak species (*Quercus*) examined with SEM for trichome morphological variation. Voucher specimens are deposited at Bailey Hortorium, Cornell University (BH).

Taxa	Voucher specimen
Q. acherdophylla Trelease	*Vázquez et al. 3065*
Q. affinis Scheidweiler	*Muller 9716*
Q. aristata Hooker & Arnott	*Martínez 31, Breedlove 1640*
Q. candicans Née	*Vázquez et al. 3095*
Q. castanea Née	*Rzedowski 25361*
Q. coahuilensis Nixon & Muller	*Stewart 924*
Q. coccolobifolia Trelease	*Vázquez & Phillips 3084*
Q. conzattii Trelease	*Muller 9420*
Q. crassifolia Humboldt & Bonpland	*Vázquez et al. 3049*
Q. crassipes Humboldt & Bonpland	*Vázquez et al. 3037, 3070*
Q. depressa Humboldt & Bonpland	*Vázquez & Tenorio 118*
Q. durifolia von Seemen	*Muller 3579*
Q. x *dysophylla* Bentham	*Nixon s.n. (Oct. 1999)*
Q. eduardii Trelease	*Nixon 4034, Vázquez et al. 3011*
Q. fulva Liebmann	*Vázquez et al. 3097*
Q. gentryi Muller	*McVaugh 25635*
Q. hintonii Warburg	*Vázquez et al. 3029*
Q. hintoniorum Nixon & Muller	*Eckelman 21, Poole 2336*
Q. hirtifolia Vázquez, Valencia & Nixon	*Vázquez et al. 3069, 3109*
Q. hypoleucoides Camus	*Yen & Estrada 8338*
Q. hypoxantha Trelease	*Cowan et al. 5402*
Q. mcvaughii Spellenberg	*Bacon et al. 5284*
Q. mexicana Humboldt & Bonpland	*Rzedowski 6374*
Q. planipocula Trelease	*McVaugh12136*
Q. radiata Trelease	*Rzedowski 23018*
Q. salicifolia Née	*McVaugh 25456*
Q. scytophylla Liebmann	*Vázquez et al. 3035*
Q. sideroxyla Humboldt & Bonpland	*Vázquez et al. 3089, Bacon et al. 5304*
Q. tarahumara Spellenberg, Bacon & Breedlove	*Bacon et al. 5307, 5375*
Q. urbanii Trelease	*Vázquez et al. 3027*

red oak species endemic to Mexico were included. Samples of the materialexamined were gathered from field collections and from herbarium specimens deposited at the Bailey Hortorium, Cornell University (BH) (Table 1).

Twenty to thirty specimens per species were initially examined under dissecting and light microscopy to survey the intra- and interspecific variation in trichome morphology. A more detailed examination was carried out under SEM in representative subsamples. About one square cm of the abaxial surface of a dry leaf or one cm of twig was mounted on an aluminum stub with no prior treatment. Previous studies have shown no difference in the preservation of nonglandular trichome structure using either fresh or dry tissue (Hardin 1976). Specimens mounted on stubs were sputter coated with 30 nm of gold palladium using a BAL-TEC sputter coater. Samples were observed under a Zeiss electron microscope, model LEO DSM 960, using working distances between 12 and 18 mm, voltages of 3.0 or 4.0 kV, and apertures of 300 μm or 400 μm depending on the sample and magnification. Most trichome micrographs were taken at magnifications of 200×, although smaller trichomes required magnifications of 450–500×.

TABLE 2. Trichome types on twigs of Mexican red oak species (*Quercus*).

Species	Glandular		Nonglandular			
	Simple uniseriate	Branched	Fasciculate sessile simple	Fasciculate stipitate	Multiradiate	Simple Stellate
Q. acherdophylla	X					X
Q. affinis					X	
Q. aristata				X		
Q. candicans			X		X	X
Q. castanea			X			
Q. coahuilensis			X	X		
Q. coccolobifolia	X		X			
Q. conzattii			X		X	
Q. crassifolia	X		X	X		
Q. crassipes			X		X	
Q. depressa					X	
Q. durifolia			X		X	
Q. × *dysophylla*			X	X		
Q. eduardii			X		X	
Q. fulva			X		X	
Q. gentryii					X	
Q. hintonii			X		X	
Q. hintoniorum			X		X	
Q. hirtifolia			X	X		
Q. hypoleucoides			X		X	
Q. hypoxantha			X		X	
Q. mcvaughii			X		X	
Q. mexicana			X		X	
Q. planipocula			X			
Q. radiata			X			
Q. salicifolia		X				
Q. scytophylla			X		X	
Q. sideroxyla			X		X	
Q. tarahumara			X			
Q. urbanii			X		X	

RESULTS

Trichome nomenclature follows Hardin (1976), where each cell composing a nonglandular trichome is called a "ray" and trichome types are named based on the degree of ray fusion, ray orientation, and overall morphology. However, additional terms have been introduced to describe trichome types not previously reported in the literature.

Two general trichome categories are used to indicate secretory functions and nature of the cell wall: 1) glandular trichomes have a glistening appearance and thin cell walls that collapse upon drying, and 2) nonglandular trichomes lack a glistening appearance and possess thick cell walls. Examination of twigs and abaxial leaf surfaces of thirty red oak species resulted in two types of glandular trichomes and eight nonglandular trichome types (Tables 2 and 3).

Glandular trichomes

1. *Simple uniseriate (Fig. 1A, 1B).*—This type consists of 2–7 united cells with slight constrictions along the trichome length. This trichome type was commonly found on

Table 3. Trichome types in oak species (*Quercus*) with a persistent indumentum on the abaxial leaf surfaces.

Species	Glandular		Nonglandular							
	Simple uniseriate	Branched	Fasciculate sessile simple	Fasciculate sessile contorted	Fasciculate sessile crested	Fasciculate stipitate	Multi-radiate	Simple stellate	Fused stellate	Multiple stellate
Q. acherdophylla						Xv				
Q. affinis						Xv				
Q. aristata			X			X				
Q. candicans	X						X	X	X	
Q. castanea	X		X							
Q. coahuilensis	X		X							
Q. coccolobifolia	X					Xv				
Q. conzattii						X				
Q. crassifolia	X		X			X				
Q. crassipes	X					X				
Q. depressa						Xv				
Q. durifolia							X	X		
Q. × dysophylla	X					X				
Q. eduardii				X						
Q. fulva	X						X			
Q. gentryi	X							X		Xs
Q. hintonii	X		X			X				
Q. hintoniorum	X					Xv	X			
Q. hirtifolia			X			X				
Q. hypoleucoides	X						X			
Q. hypoxantha	X		X							
Q. mcvaughii	X		X							
Q. mexicana	X			X						
Q. planipocula	X					X				
Q. radiata	X		X							
Q. salicifolia		Xs					Xs			
Q. scytophylla	X						X			
Q. sideroxyla	X				X		X			
Q. tarahumara	X		X			X				
Q. urbanii	X					X				

s=scattered **v**=trichomes on secondary veins

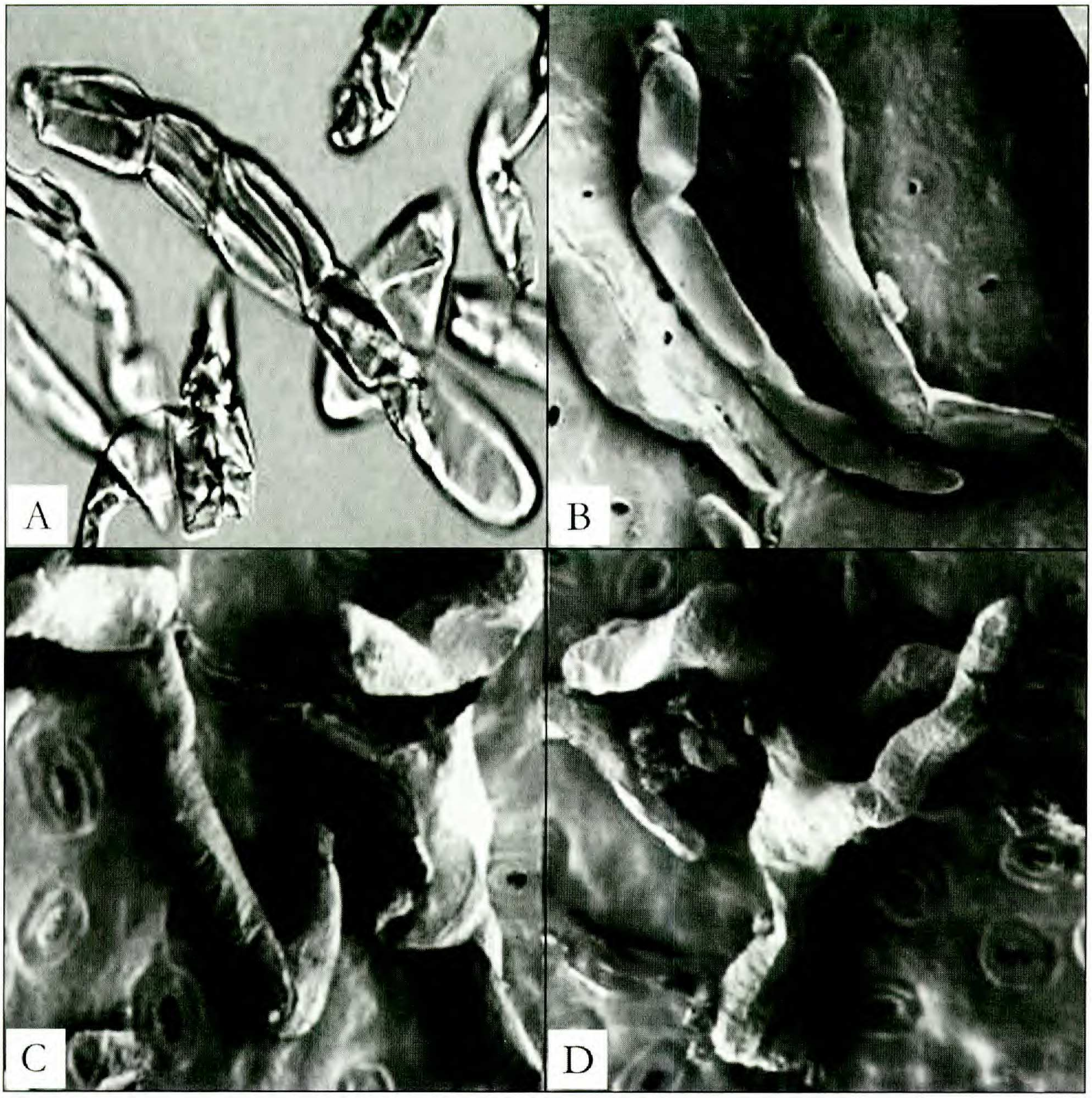

FIG. 1. **A.** Thin cell wall in a glandular trichome of *Quercus coccolobifolia*. ×40. **B.** Glandular simple uniseriate trichome on the abaxial leaf surface of *Q. hintoniorum*, ×500. **C.** Glandular branched trichome on the abaxial surface of *Q. salicifolia*, ×500. **D.** A variation of the glandular branched trichome on the abaxial leaf surface of *Q. salicifolia*, ×500.

the abaxial leaf surfaces of twenty-one species, forming a sparse and deciduous indumentum. In most species examined, trichome density decreased during leaf maturation and senescence; however, *Quercus coccolobifolia* showed persistent simple uniseriate trichomes on the abaxial leaf surface. This trichome type was found on the twigs of only three species: *Q. acherdophylla*, *Q. coccolobifolia*, and *Q. crassifolia* (Table 2).

2. *Branched* (Fig. 1C, 1D).—This type consists of 2–3 cells united in either a V or a Y shape; however, under the dissecting microscope this trichome type looks like two unicellular simple trichomes lying next to each other. This trichome type was found exclusively on abaxial surfaces of *Q. salicifolia* leaves.

Nonglandular trichomes

Fasciculate sessile trichomes.—These consist of several rays fused at the point of attachment to the epidermis. The rays are either short and completely erect (Fig. 2A), or long

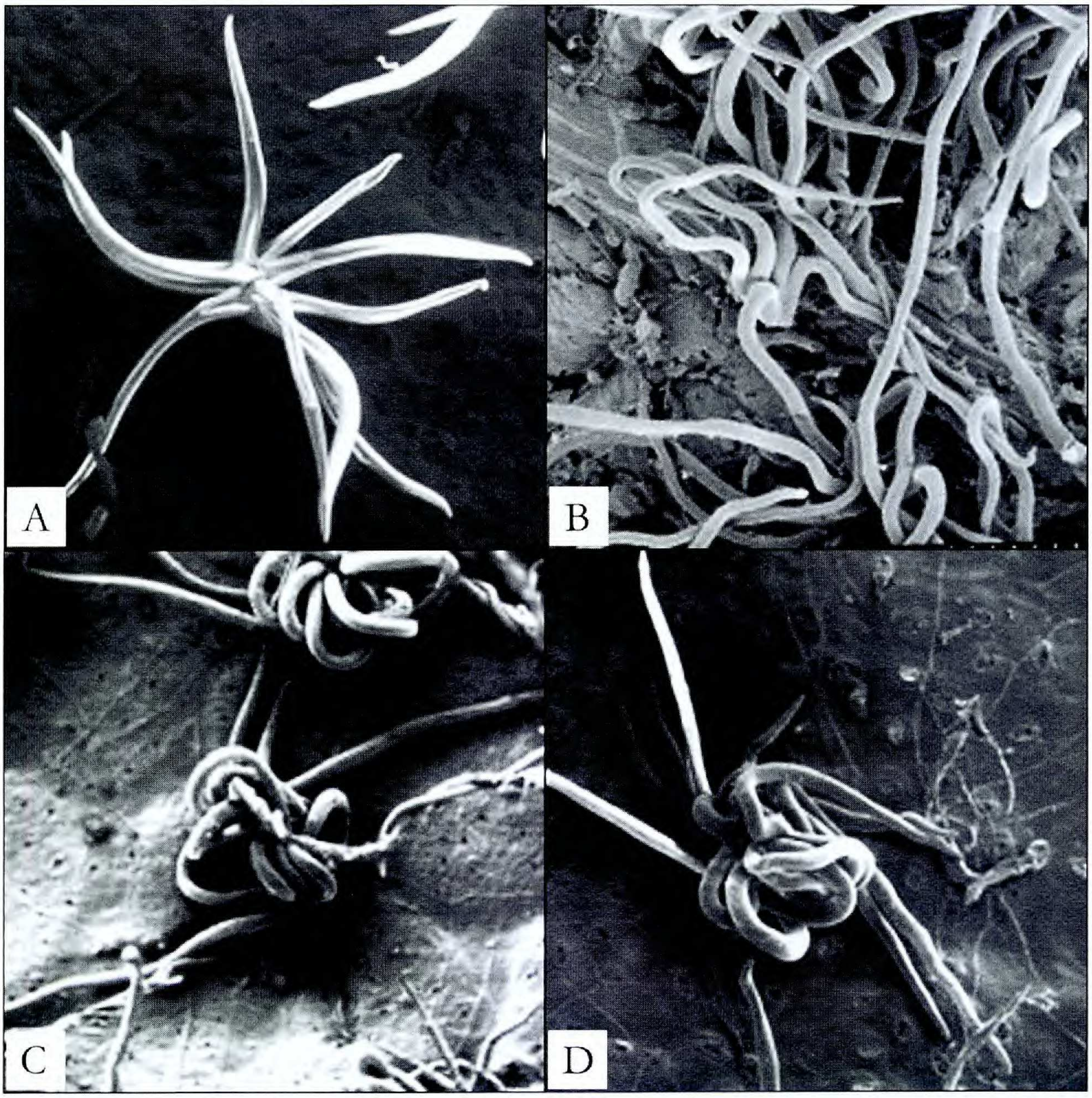

Fig. 2. A. Fasciculate sessile simple trichome on the abaxial leaf surface of *Quercus aristata,* ×200. **B.** Fasciculate sessile simple trichome on the abaxial leaf surface of *Q. crassifolia,* ×200. **C.** Fasciculate sessile contorted trichome on the abaxial leaf surface of *Q. mexicana,* ×200. **D.** Fasciculate sessile contorted trichome on the abaxial leaf surface of *Q. eduardii* ×200.

and tortuous diverging in different directions (Fig. 2B). Three types of fasciculate sessile trichomes are recognized in the species examined.

1. Fasciculate sessile simple (Fig. 2A, 2B).—The fasciculate sessile trichome described by Hardin (1976; 1979a) and Jones (1986) is termed here fasciculate sessile simple to distinguish it from the two additional subtypes listed below. This trichome type was found on twigs and/or on the abaxial leaf surfaces of several species examined. It occurs on twigs of the following species: *Q. candicans, Q. castanea, Q. coahuilensis, Q. coccolobifolia, Q. conzattii, Q. crassifolia, Q. crassipes, Q. durifolia, Q.* x *dysophylla, Q. eduardii, Q. fulva, Q. hintonii, Q. hintoniorum, Q. hirtifolia, Q. hypoleucoides, Q. hypoxantha, Q. mcvaughii, Q. mexicana, Q. planipocula, Q. radiata, Q. scytophylla, Q. sideroxyla, Q. tarahumara* and *Q. urbanii.* Species bearing this trichome type on abaxial leaf surfaces are *Q. aristata, Q. castanea, Q. coahuilensis, Q. crassifolia, Q. hintonii, Q. hirtifolia, Q. hypoxantha, Q. mcvaughii, Q. radiata,* and *Q. tarahumara* (Table 2).

2. *Fasciculate sessile contorted (Figs. 2C, 2D).*—This study describes this trichome type for the first time. Contorted trichomes are similar to the fasciculate sessile simple trichome described above except that the rays curl down and then twist around the trichome axis. This ray arrangement gives the indumentum a punctate appearance when observed with the naked eye or at low magnification. This trichome type has been found on the abaxial leaf surface of only two species of Mexican red oaks: *Q. mexicana* and *Q. eduardii*.

3. *Fasciculate sessile crested (Fig. 3A).*—This is a new trichome type that consists of rays united along a longitudinal axis oriented parallel to the epidermis. The united rays result in a structure that resembles a crest. Trichomes of this type were found only on the abaxial surface of some *Q. sideroxyla* specimens.

4. *Fasciculate stipitate (Figs. 3B, 3C).*—Morphologically, this trichome type is similar to the fasciculate sessile simple except that the basal parts of the rays fuse, forming a stipe. The degree of ray fusion varies among species from 1/12 to 1/4 the total ray length. Ray length and degree of divergence are also different; some species display short and straight rays (Fig. 3B) while others show long curly rays that become intertwined with adjacent rays (Fig. 3C). Ray number is variable within and among species, although intraspecific ranges are low. Fasciculate stipitate trichomes form a persistent indumentum on the abaxial leaf surface of the following species: *Q. conzattii*, *Q. crassifolia*, *Q. crassipes*, *Q.* x *dysophylla*, *Q. hintonii*, *Q. hirtifolia*, *Q. planipocula*, *Q. tarahumara*, and *Q. urbanii*. In *Q. aristata*, fasciculate stipitate trichomes are deciduous and scattered on the abaxial leaf surface. In many otherwise glabrous species, such as *Q. acherdophylla*, *Q. affinis*, *Q. coccolobifolia*, *Q. depressa*, and *Q. hintoniorum*, only a few fasciculate stipitate trichomes remain attached to the epidermis at the secondary vein axils. Fasciculate stipitate trichomes on twigs were less common and found only in *Q. aristata*, *Q. coahuilensis*, *Q. crassifolia*, *Q.* x *dysophylla* and *Q. hirtifolia*.

5. *Multiradiate (Figs. 3D, 4A, 4B).*—This trichome type is characterized by the divergence of rays in different directions from the central axis. In the species examined, the rays differ not only in length but also in thickness. Multiradiate trichomes were found on both twigs and abaxial leaf surfaces of *Q. candicans*, *Q. durifolia*, *Q. fulva*, *Q. hintoniorum*, *Q. hypoleucoides*, *Q. scytophylla*, and *Q. sideroxyla*. This trichome type was found only on the twigs of the following species: *Q. affinis*, *Q. conzattii*, *Q. crassipes*, *Q. depressa*, *Q. eduardii*, *Q. gentryi*, *Q. hintonii*, *Q. hypoxantha*, *Q. mcvaughii*, *Q. mexicana*, and *Q. urbanii*. Multiradiate trichomes occurring on abaxial leaf surfaces usually form a persistent indument; however, in *Q. salicifolia* these trichomes are found scattered sparsely across the lamina.

6. *Simple stellate (Figs. 4C, 4D, 5A).*—This trichome type consists of rays appressed to the lamina, usually fused at their base, forming a structure that resembles a starfish. Simple stellate trichomes are composed of seven to fifteen rays, which vary in length, thickness, and size. This trichome type was previously described by Hardin (1976) and Jones (1986) under the term stellate. Here the term simple stellate is used to set it apart from the multiple stellate and fused stellate also found in this study. Simple stellate trichomes were found on the twigs of *Q. acherdophylla*, and *Q. candicans*, as well as on the abaxial leaf surfaces of *Q. candicans*, *Q. durifolia* and *Q. gentryi*.

7. *Multiple stellate (Fig. 5B).*—This new trichome type consists of 2–3 stellate trichomes joined together forming a trichome cluster. It was found only on one species, scattered on the abaxial leaf surface of *Q. gentryi*.

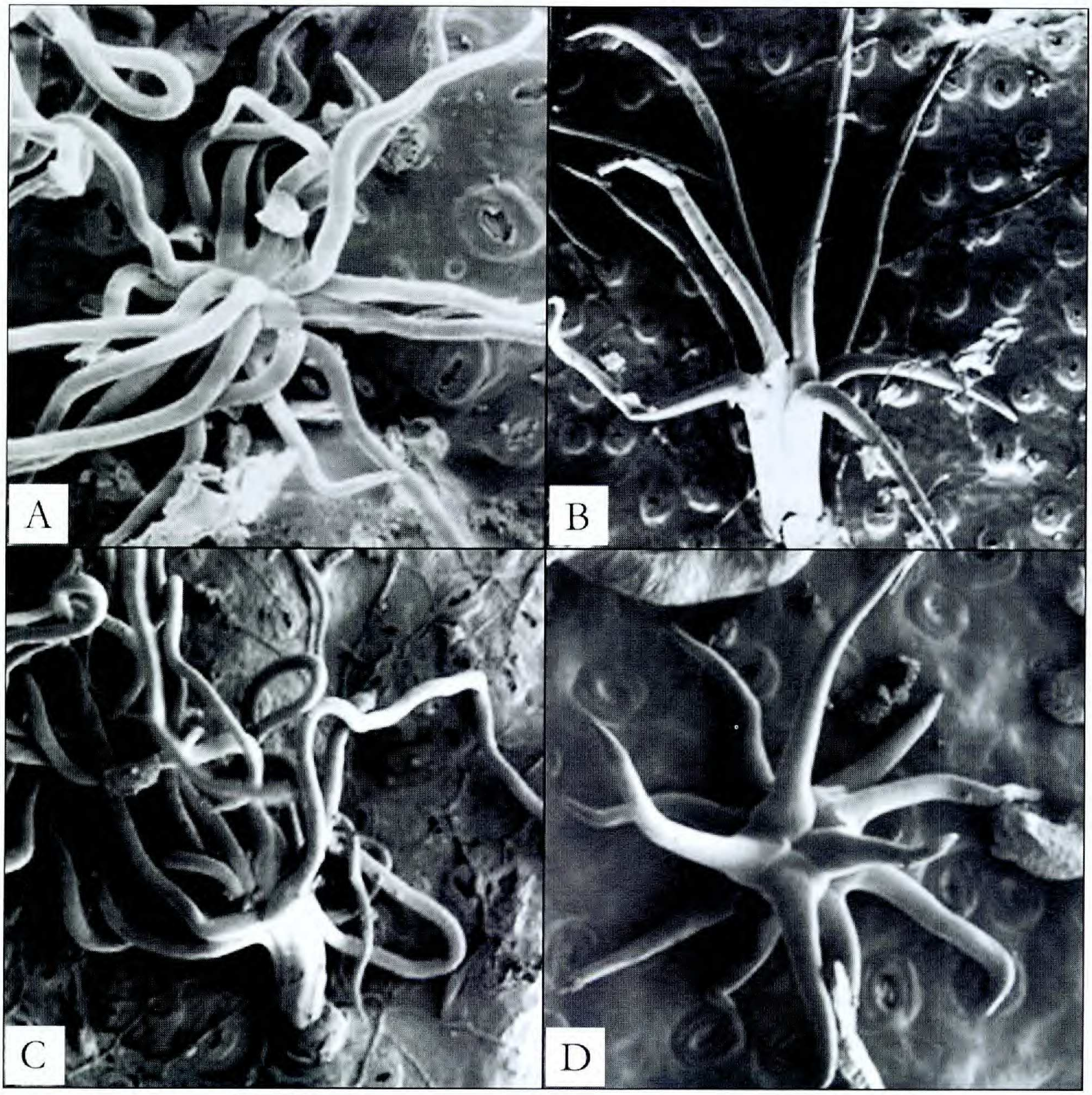

FIG. 3. **A.** Fasciculate sessile crested trichome on the abaxial leaf surface of *Quercus sideroxyla,* ×450. **B.** Fasciculate stipitate trichome on the abaxial leaf surface of *Q. aristata,* ×200. **C.** Fasciculate stipitate trichome on the abaxial leaf surface of *Q. conzatti* ×200. **D.** Multiradiate trichome on the abaxial leaf surface of *Q. salicifolia,* ×500.

8. *Fused stellate* (*Fig. 5C*).—This trichome type previously described by Hardin (1979a) and Jones (1986) consists of rays fused about one sixth of the ray length. This trichome type, not previously reported for red oaks, was found exclusively on the abaxial leaf surface of *Q. candicans.*

DISCUSSION

The study of trichomes with SEM revealed significant differences in trichomes that appeared similar when viewed with dissecting microscopy. These differences have allowed a more accurate characterization of trichome types and have also led to the discovery of three new nonglandular trichome types: fasciculate contorted, fasciculate crested, and multiple stellate. Fasciculate contorted trichomes, although recognized as a different type by several authors (McVaugh 1974; González 1986), had been included under the stellate

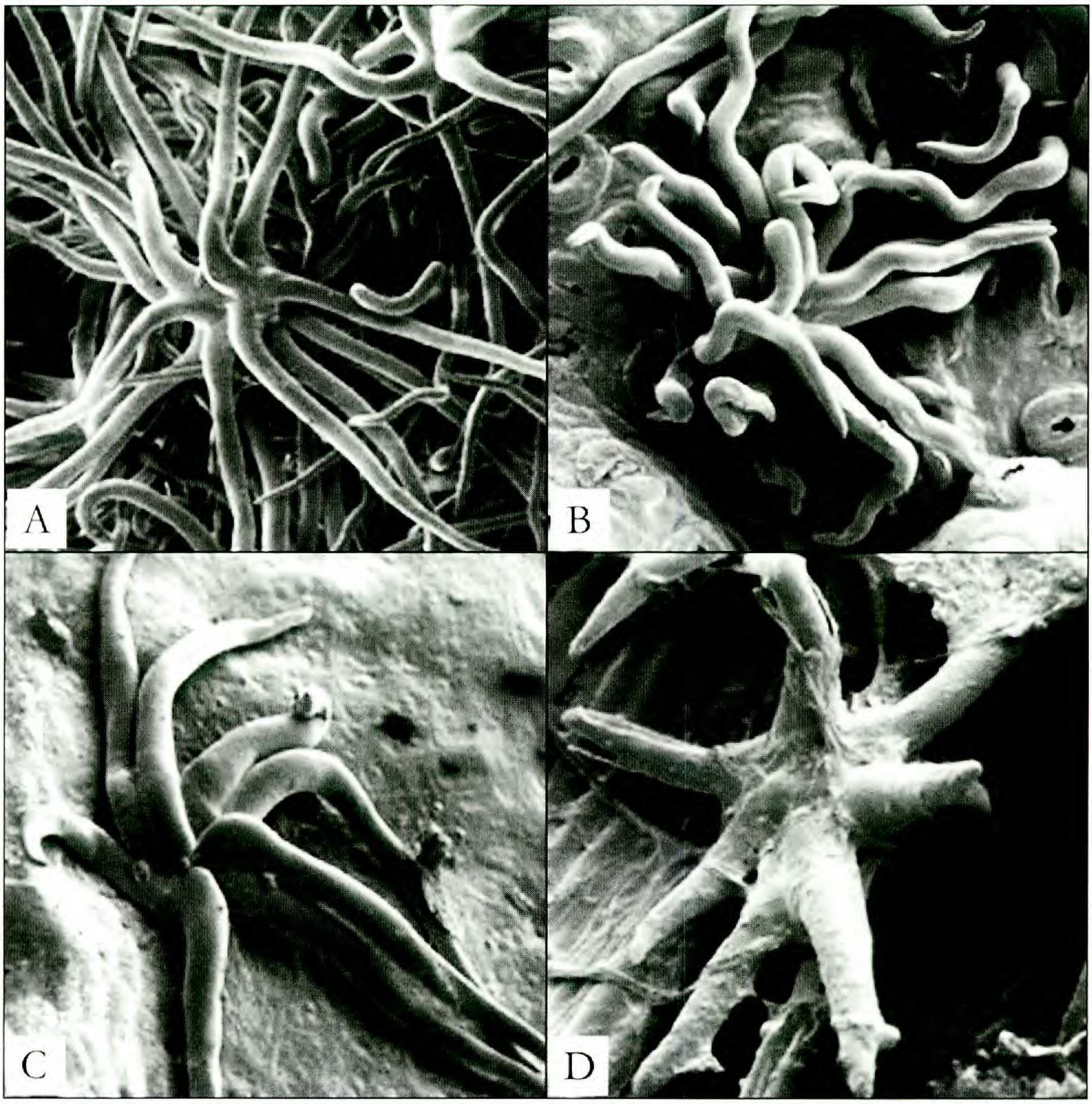

Fig. 4. A. Multiradiate trichome on the abaxial surface of *Quercus durifolia,* ×300. **B.** Multiradiate trichome on the abaxial leaf surface of *Q. scytophylla,* ×500. **C.** Simple stellate trichome on the adaxial leaf surface of *Q. eduardii* ×500. **D.** Simple stellate trichomes on the twigs of *Q. acherdophylla* ×800.

type. The second new trichome type, fasciculate simple crested, is found only on the abaxial leaf surface of some *Q. sideroxyla* specimens. The uncommon distribution of fasciculate crested trichomes suggests that they could represent a variation of the multiradiate type, which is an abundant trichome type in the indumentum of *Q. sideroxyla*. The third new trichome type, multiple stellate, is found in a scattered pattern exclusively on the abaxial leaf surface of *Q. gentryi*. Under the dissecting microscope this trichome resembles a multiradiate type but close examination with SEM reveals that it consists of two to three stellate trichomes fused together (Fig. 5B). Therefore, trichomes that appear multiradiate must be examined carefully to avoid inclusion of multiple stellate types into this category. For example, Hardin (1979b) described a trichome type as a dense multiradiate, however, his corresponding illustration (Fig. 30) shows a morphological resemblance to the multiple stellate type described here.

In addition to the new trichome types found in this study, three types represent new

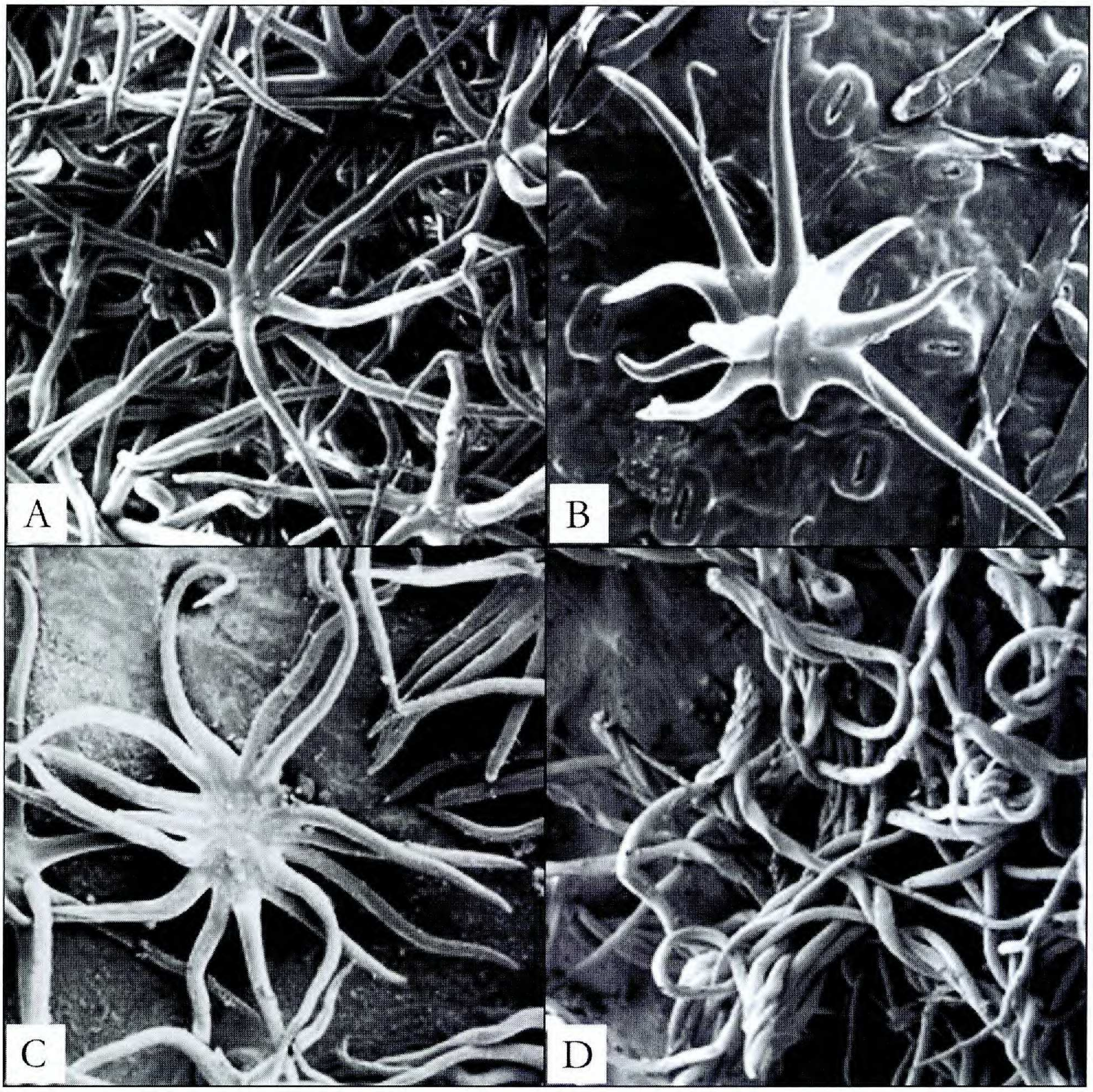

Fig. 5. A. Simple stellate trichomes on the abaxial leaf surface of *Quercus durifolia* ×250. **B.** Multiple stellate trichomes on lower leaf surface of *Q. gentryii* _450. **C.** Fused stellate trichomes on the abaxial leaf side of *Q. candicans*, ×200. **D.** Fasciculate sessile trichomes with twisted rays on the abaxial leaf side of *Q. coahuilensis*, ×150.

reports for red oaks: stellate, fused stellate, and glandular branched. Previous research had indicated that stellate and fused stellate types occurred only in white oaks (Hardin 1979a); however, this study found these trichome types in *Q. candicans*. Jones (1986) stated that stellate trichomes are "usually restricted to large veins or sometimes only the petiole." In this research, stellate trichomes were found forming a dense and persistent indumentum on the abaxial leaf surfaces of the aforementioned species. The glandular branched type was rare and only found on the abaxial leaf surface of *Q. salicifolia*. This result supports Hardin's statement (1976) that this trichome type is not very common in red and white oaks.

SEM was also useful in the accurate identification of previously known trichome types. For example, at low magnifications, trichomes on the abaxial leaf surface of *Q. coahuilensis* appear fasciculate stipitate, but examination under SEM has revealed that they are fasciculate sessile: the stipe-like structure is formed by the twisting of rays near the trichome base (Fig. 5D). Similarly, detailed study of the trichome type denoted as "starred" in several descriptions of Mexican oak species (Bello & Labat 1987; Valencia 1989; Vázquez 1992, 2000; Romero 1993) showed that these categories correspond to four different trichome types: fasciculate sessile, fasciculate stipitate, fasciculate contorted, or multiradiate trichomes. Acknowledging the trichome variation included under the term "starred" will facilitate future characterization of Mexican oak taxa.

Study of twigs under SEM has also revealed remarkable characteristics regarding the nature of the indumentum. Several taxonomic treatments of Mexican oak taxa (González 1986; Valencia 1989; Vázquez 1992) imply that the twig indumentum consists of only one nonglandular trichome type. However, the results of this study indicate that the indumentum of nineteen of the species examined is composed of two to three trichome types arranged in overlapping layers (Fig. 6A). Of the thirty species examined, only nine have a twig indumentum composed of one nonglandular trichome type (Figs. 6B, 6C).

In general, species bearing more than one nonglandular trichome type on twigs and/or leaves show several combinations of glandular and nonglandular trichomes, termed trichome complements. Glandular trichome types are not included in the trichome complements because, if present, they usually are deciduous.

Trichome complements on twigs

The most common trichome complement on twigs is multiradiate/fasciculate sessile simple and occurs in the following species: *Q. conzattii*, *Q. crassipes*, *Q. durifolia*, *Q. eduardii*, *Q. fulva*, *Q. hintonii*, *Q. hintoniorum*, *Q. hypoleucoides*, *Q. hypoxantha*, *Q. mcvaughii*, *Q. mexicana*, *Q. scytophylla*, *Q. sideroxyla*, and *Q. urbanii*. Twigs with a trichome complement consisting of fasciculate sessile simple/fasciculate stipitate trichomes are found in *Q. coahuilensis*, *Q. crassifolia*, *Q.* × *dysophylla*, and *Q. hirtifolia*. A species-specific trichome complement was found on twigs of *Q. candicans* (fasciculate sessile simple/multiradiate/simple stellate) (Table 2).

Trichome complements on the abaxial surface of leaves

The distribution of glandular trichomes on leaves showed different patterns. On one hand, the simple branched glandular trichome type is found exclusively on the abaxial leaf surface of *Q. salicifolia* in a scattered fashion (Fig. 6D). On the other hand, the simple uniseriate type is found on the abaxial leaf surface of most of the species examined. Generally, this trichome is deciduous and usually not found on mature leaves; however, in *Q. radiata* and *Q. coccolobifolia*, these glandular trichomes are persistent in the form of mucilaginous droplets, which according to Uphof (1962) are the result of decaying glandular trichomes. The common presence of simple uniseriate glandular trichomes has also been documented for many US and European oak species (Hardin 1976, 1979a; Llamas et al. 1995), and has also been found in the red oak species examined here.

Trichome complements on the abaxial leaf surface are composed of two to four trichome types (Table 3). The trichome complement fasciculate sessile simple/fasciculate stipitate is found in the species *Q. aristata*, *Q. crassifolia*, *Q. hintonii*, *Q. hirtifolia*, and *Q. tarahumara*. Species-specific trichome complements are present on the abaxial leaf surface of *Q. candicans* (multiradiate/simple stellate/fused stellate), *Q. durifolia* (multiradiate/simple stellate), *Q. hintoniorum* (fasciculate stipitate/multiradiate), and *Q. sideroxyla* (fasciculate sessile crested/multiradiate), (Table 3). Although the occurrence of more than one nonglandular trichome type on the abaxial surface has been documented for European

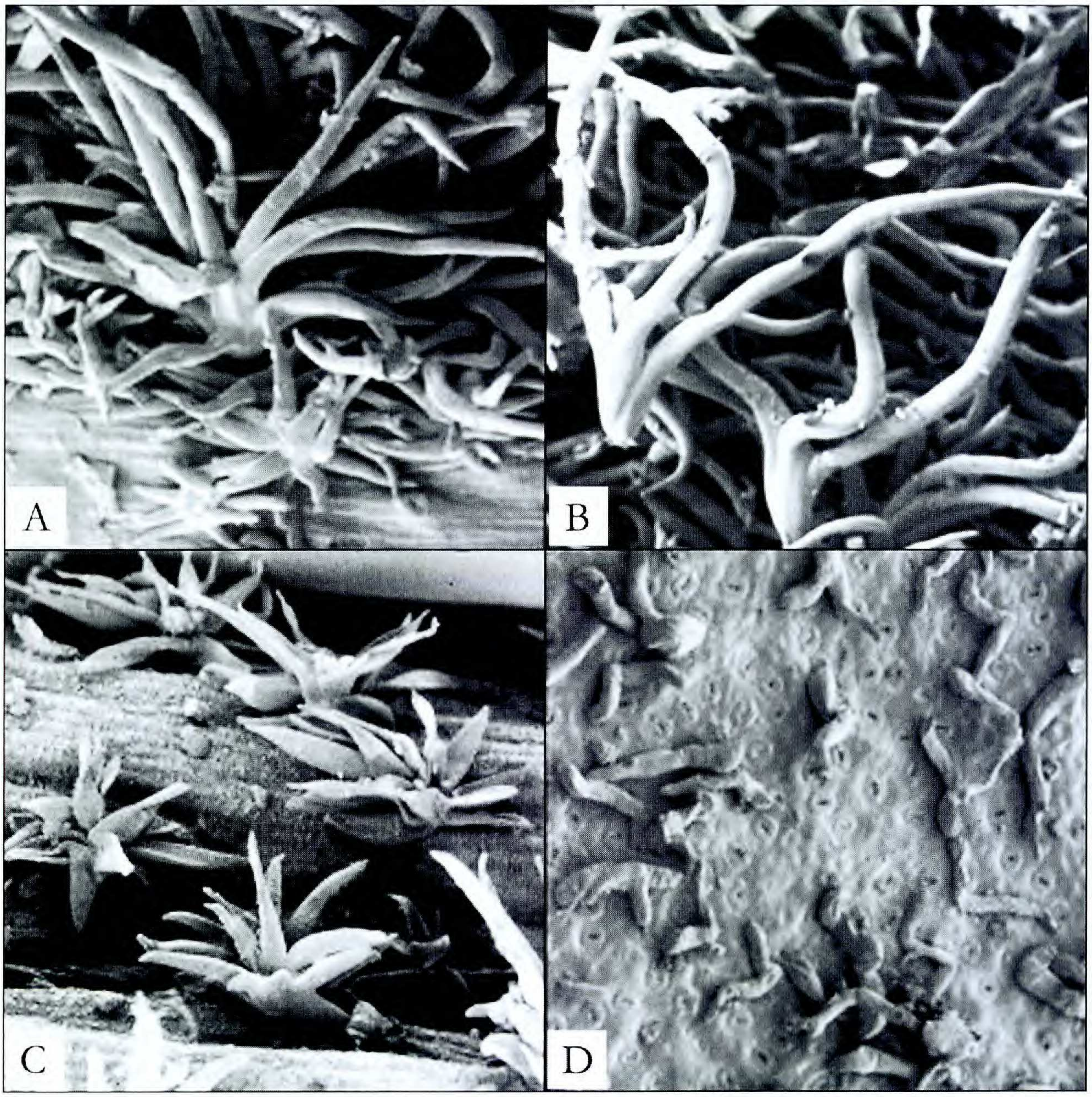

Fig. 6. A. Fasciculate and stellate trichomes on the twig of *Quercus candicans*, ×200. **B.** Fasciculate sessile simple (left) or shortly stipitate (right) trichomes on twigs of *Q. hintonii*, ×200. **C.** Multiradiate trichomes on the twigs of *Q. affinis* ×200. **D.** Scattered branched glandular trichomes on the abaxial leaf surface of *Q. salicifolia*, ×200.

(Safou & Saint-Martin 1989) and North American (Thomson & Mohlenbrock 1979) oak species, it has only been described for a few Mexican taxa. For example, Nixon and Muller (1993) described the unique trichome complement found in *Q. hintoniorum* and related species.

The abaxial leaf surface of six of the included species is essentially glabrous except for clusters of fasciculate stipitate trichomes in the vein axils, or scattered multiradiate or stellate trichomes distributed throughout the lamina. Species with fasciculate stipitate trichomes restricted to vein axils are: *Q. acherdophylla*, *Q. affinis*, *Q. depressa*, and *Q. coccolobifolia*, although the later species also has abundant simple uniseriate trichomes throughout the abaxial surface. Scattered multiple stellate and multiradiate trichomes have been found only in *Q. gentryi* while dispersed multiradiate and branched glandular trichomes are found in *Q. salicifolia*.

Trichome morphology and species identification

There are several instances where trichome morphology can be a valuable tool in the identification of red oak species, especially of those with similar overall features. For example, *Q. crassipes* and *Q. mexicana* (Figs. 7A, B) are frequently confused because they have similar leaf morphology. However, examination of trichomes on the abaxial leaf surfaces reveals clear differences: while *Q. crassipes* has fasciculate stipitate trichomes, *Q. mexicana* shows fasciculate sessile contorted trichomes. Reproductive characters (e.g. fruit morphology) agree with their distinctiveness based on trichome morphology. Another example of the utility of trichome morphology for species identification is found in the *Crassifoliae* complex (sensu Vázquez 2001), which consists of fourteen species characterized by the presence of a pale-yellow indumentum on the abaxial leaf surface, and by a morphological resemblance to leaves of *Q. crassifolia*. Two species often confused with *Q. crassifolia* are *Q. mcvaughii* and *Q. fulva*. While the abaxial leaf surface of *Q. crassifolia* has distinctive fasciculate stipitate trichomes, *Q. mcvaughii* displays fasciculate sessile trichomes and *Q. fulva* shows multiradiate trichomes on their abaxial leaf surfaces. In fact, trichome differences between *Q. crassifolia* and *Q. mcvaughii*, together with other morphological and reproductive characters were used in the segregation of these morphologically similar species (Spellenberg 1992).

A potential problem in trichome classification is that there are cases when there is not a clear-cut distinction among types. One case involves Hardin's (1976) glandular rosulate trichome type, characterized by the rosette pattern of the rays and, most importantly, the rays having a thin cell wall. In practice, it is difficult to determine the nature of the cell wall unless ultrastructural studies are carried out. In the absence of such studies and taking into account ray arrangement, these trichomes should be classified as multiradiate. In this study, all trichomes with rays originating from a single point and diverging in different directions were considered within the multiradiate type.

A second problem in the identification of trichome types is the transition of one type into another. In the specimens examined, morphological transitions were observed between fasciculate sessile and fasciculate stipitate trichomes, and from fasciculate sessile to stellate. These examples agree with Jones' (1986) statement that sometimes there are no discrete boundaries between trichome types and that "...most forms intergrade with at least one other type ..."

Despite these potential limitations, SEM has been a key factor in the discovery of three new trichome types, as well as in the finding of three trichome types not previously reported for red oaks. Furthermore, study of trichomes under SEM has revealed key morphological differences in apparently similar trichome types. Detailed examination of trichomes from Mexican oak taxa revealed that four different trichome types had been included under the "starred" category in the taxonomic literature. The trichome complements of mature leaves are useful in the identification of morphologically similar oak species when taken together with other vegetative and reproductive features, as indicated in the dichotomous key below. This work provides a standard terminology that could be used in future taxonomic treatments to aid in species circumscription of Mexican oak taxa.

DICHOTOMOUS KEY FOR IDENTIFICATION OF MEXICAN RED OAK SPECIES

1. Abaxial leaf surface either completely devoid of trichomes or appearing glabrous except for scattered glandular or nonglandular trichomes.
   2. Leaf shape ovate to suborbicular or pandurate; abaxial leaf surface with abundant simple

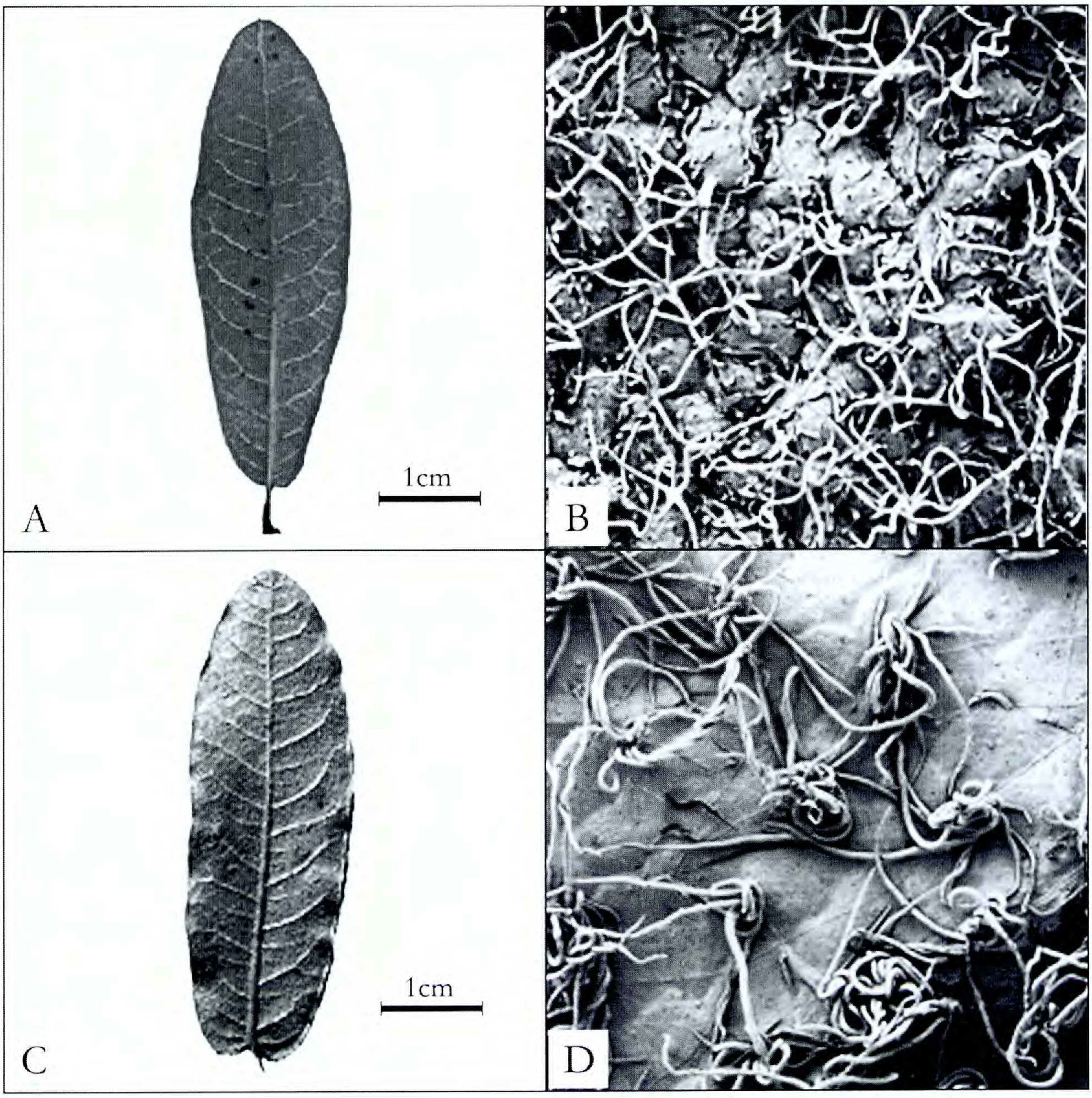

Fig. 7. A.–B. ***Quercus crassipes,*** **left, mature leaves; right, fasciculate stipitate trichome on the abaxial leaf surface, ×74. C.–D.** ***Q. mexicana*** **left, mature leaves; right, fasciculate sessile contorted trichomes on the abaxial leaf surface ×74.**

uniseriate glandular trichomes and a few fasciculate stipitate trichomes restricted to the secondary vein axils ____________________ **Q. coccolobifolia**

2. Leaf shape elliptic, lanceolate, ovate-lanceolate, or oblanceolate; abaxial leaf surface devoid of trichomes or with scattered stellate or multiradiate trichomes.
   3. Leaf margin entire and undulate.
      4. Leaves 4–6 times long as wide; abaxial leaf surface with sparse multiple stellate trichomes or multiradiate trichomes distributed throughout the lamina and vein axils; fruits with biennial maturation.
         5. Secondary veins 10–15; two-thirds of the acorn included in the cup; epidermis on the abaxial leaf surface bullate ____________________ **Q. gentryi**
         5. Secondary veins 15–25; one-third of the acorn included in the cup; epidermis on the abaxial leaf surface smooth ____________________ **Q. salicifolia**
      4. Leaves 2–2.5 times long as wide, abaxial leaf surface lacking trichomes on the lamina but with fasciculate stipitate trichomes on the vein axils; fruits with annual maturation ____________________ **Q. acherdophylla**

3. Leaf margin entire and straight or with short teeth.
6. Leaf base attenuate, cuneate or decurrent; mature leaves 3.6–4.2 times long as wide ____ **Q. affinis**
6. Leaf base round or obtuse; mature leaves 2.4–2.6 long as wide ____ **Q. depressa**
1. Abaxial leaf surface with abundant and persistent nonglandular trichomes, sometimes trichomes detaching with age.
7. Abaxial leaf surface sparingly pubescent or glabrescent; if sparingly pubescent, at low magnifications the epidermis could be seen through the trichomes.
8. Trichomes on abaxial leaf surface have a punctate appearance; trichomes fasciculate contorted.
9. Leaves elliptic-oblong, always entire, veins 6–16 ____ **Q. mexicana**
9. Leaves elliptic-lanceolate, elliptic-oblanceolate, sometimes obovate or ovate, entire or toothed, veins 5–8 ____ **Q. eduardii**
8. Trichomes on abaxial leaf surface have a floccose or arachnoid appearance; trichomes fasciculate stipitate, fasciculate sessile simple, or multiradiate.
10. Leaves orbicular, orbicular-pandurate, or broadly obovate; twigs 4–8 mm thick.
11. Mature leaves with 4–8 teeth; infructescence up to 6 mm long bearing 1–2 fruits ____ **Q. tarahumara**
11. Mature leaves with 13–19 teeth; infructescence from 4.7 to 15 cm long bearing 3–9 fruits ____ **Q. radiata**
10. Leaves elliptic, lanceolate, ovate or obovate; twigs 0.75–4(–5) mm thick.
12. Fruit cupule with the margin involute; cupule diameter 20–28 mm; secondary veins 10–19 ____ **Q. planipocula**
12. Fruit cupule with the margin straight; cupule diameter 7–15 mm; secondary veins 4–12.
13. Fruits with annual maturation; bullate epidermis on the abaxial leaf surface; secondary veins 5–12.
14. Leaves obovate to elliptic; trichomes on the abaxial leaf surface fasciculate sessile or fasciculate shortly stipitate; leaf margin toothed; distributed in the Sierra Madre Oriental ____ **Q. hirtifolia**
14. Leaves elliptic-lanceolate, elliptic-oblanceolate, sometimes obovate or ovate; trichomes on the abaxial leaf surface fasciculate distinctly stipitate; leaf margin entire or entire-aristate; distributed in the Sierra Madre Occidental ____ **Q. aristata**
13. Fruits with biennial maturation; smooth epidermis on the abaxial leaf surface; secondary veins 4–5.
15. Abaxial leaf surface appearing glabrous but with two types of glandular nontrichomes visible at 10×: small multiradiate of short rays distributed on the abaxial lamina and fasciculate stipitate trichomes confined to the secondary vein axils ____ **Q. hintoniorum**
15. Abaxial leaf surface pubescent but the trichomes detach with age; trichomes fasciculate sessile simple with long intertwined rays distributed throughout the lamina ____ **Q. hypoxantha**
7. Abaxial leaf surface densely pubescent, the epidermis completely covered with trichomes.
16. Leaves elliptic, lanceolate, oblanceolate or ovate.
17. Leaf margin always entire without aristae
18. Abaxial leaf surface densely pubescent, the indumentum whitish, trichomes multiradiate or simple stellate but appearing fasciculate sessile at 10×; apex acute or acuminate.
19. Leaf margin flat; mature leaves 2.6–3 times long as wide; petiole 2–6 mm long ____ **Q. durifolia**
19. Leaf margin revolute; mature leaves 3.75–5 times long as wide; petiole 5–15 mm long ____ **Q. hypoleucoides**
18. Abaxial leaf surface loosely pubescent, the indumentum pale yellow, trichomes clearly fasciculate stipitate at 10×; apex rounded or obtuse.
20. Mature leaves about 2.5 times longer than wide; cupule hemispheric or tur-

binate, the cupule margin not involute; current year twigs with fasciculate sessile and fasciculate stipitate trichomes ______ **Q. × dysophylla**

20. Mature leaves 4–4.5 times longer than wide; cupule hemispheric with involute margin; current year twigs with fasciculate sessile and multiradiate trichomes ______ **Q. crassipes**

17. Leaf margin mainly toothed, rarely entire with aristae.
21. Twigs 3–5 mm thick; abaxial leaf surface with fasciculate stipitate trichomes; cup very shallow up to 5 mm tall, enclosing 1/4 of the nut ______ **Q. hintonii**
21. Twigs 1–3 mm thick; abaxial leaf surface with fasciculate sessile simple, multiradiate, or fasciculate sessile crested trichomes; cup hemispheric 5–12 mm tall, enclosing 1/3 to 1/2 of the nut.
22. Abaxial leaf surface with fasciculate sessile trichomes of 6 to 10 long intertwined rays.
23. Petioles 3–5(–7) mm long; fasciculate sessile trichomes twisted at the base and detaching with age; leaf margin slightly revolute ______ **Q. coahuilensis**
23. Petioles 5–25 mm long; fasciculate sessile trichomes not twisted at the base and persisting with age; leaf margin flat ______ **Q. castanea**
22. Abaxial leaf surface with multiradiate or fasciculate sessile crested trichomes of 20–22 short rays.
24. Leaf base decurrent or cuneate; leaf tapering toward the apex; leaf margin not revolute ______ **Q. scytophylla.**
24. Leaf base rounded, subcordate or cordate; leaf apex acute or obtuse; leaf margin revolute ______ **Q. sideroxyla**

16. Leaves obovate, suborbicular, orbicular, or very broadly elliptic.
25. The indumentum on the abaxial leaf surfaces detaches with age; twigs 0.75–1 mm thick; petioles glabrous, reddish ______ **Q. hypoxantha**
25. The indumentum on the abaxial leaf surface remains attached; twigs 2–13 mm thick; petioles densely pubescent, pubescent, or glabrescent.
26. Petioles 0.4–25 mm long; cup 7–9 mm wide, 4–5 mm tall; acorn 7–11 mm long, 6–8 mm wide ______ **Q. conzattii**
26. Petioles 25–37 mm long; cup 8–24 mm wide, 5–15 mm tall; acorn 10–24 mm long, 7–21 mm wide.
27. Twigs of the season 8–13 mm thick; infructescences 3.5 to 10 cm long bearing 6–10 fruits ______ **Q. urbanii**
27. Twigs of the season 2.5–6.0 mm thick; infructescences less than 2 cm long bearing 1–2 fruits.
28. Indumentum on the abaxial leaf surface white or pale yellow; leaves with 12–17 teeth; sparse glandular trichomes on the abaxial leaf surface ______ **Q. candicans**
28. Indumentum on the abaxial leaf surface yellow or yellow-brownish; leaves with 1–11 teeth; abundant glandular trichomes on the abaxial leaf surface.
29. Abaxial leaf surface with a felted indumentum composed of multiradiate trichomes with straight rays; rim of cupule involute ______ **Q. fulva**
29. Abaxial leaf surface with a woolly indumentum composed of fasciculate trichomes with long tortuous rays; rim of cupule straight.
30. Mature leaves deciduous; trichomes on the abaxial leaf surface fasciculate stipitate ______ **Q. crassifolia**
30. Mature leaves evergreen; trichomes on the abaxial leaf surface fasciculate sessile simple ______ **Q. mcvaughii**

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